" On the Composition and Variations of the Pelvic Plexus in
    Acanthias vulgaris."   By R. C. PUNNETT, B.A., Gonville and
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Whilst recently engaged upon the development of the pelvic plexus
in *Mustelus lævis* I was much struck with the amount of variation in
the number and position of the nerves forming it.   This led me at the
time to examine all the material which I was able to procure, and the
results obtained have been given in a previous paper (12, 1900).
Believing, however, that, in Bateson's words, "the facts of variation
must be the test of phylogenetic possibility" (4, p. 30), I determined
to examine a still larger number of specimens of some other species of
shark.   The only two species in this country which from their abund-
ance lend themselves to such an investigation are *Scyllium canicula* and
Acanthias vulgaris.   The former possesses certain advantages in that it
would be possible to institute comparisons with the nearly allied
S. catulus which co-exists with it in the same locality.   Such ad-
vantages, however, are to some extent discounted by the greater
difficulties which *Scyllium* presents in working.   Owing to the greater
abundance and toughness of the connective tissue it is not nearly
such a favourable object for investigation of this kind as *Acanthias.*
This is also the case with the embryos—those of *Acanthias* giving far
clearer preparations with the gold chloride method mentioned below
than the *Scyllium* embryos.   The presence of a large " nervus col-
lector " in *Acanthias* also gives it an advantage over *Scyllium* where
the " collector " is usually represented only by a single branch.

The research was carried on at Plymouth in the summer of 1899
and of 1900, whilst occupying at the Laboratory tables both from the
British Association and from Cambridge University.   To the autho-
rities of the Biological Station I would express my thanks for the ample
supply of material forthcoming.   I also take this opportunity of
expressing my gratitude to Dr. Gadow for the kind sympathy which he
has shown during the course of the work.

The anatomy of the pelvic plexus of *Acanthias vulgaris* has been
studied by Davidoff (1) and by Braus (10).   Davidoff's account may
be briefly summarised as follows :—

The pelvic fin is innervated by seventeen nerves whose serial
numbers are 31—47.   Of these nerves 40—47 each divide on reaching
the fin, into a dorsal and a ventral portion which innervate respectively
the fin musculature lying dorsally and ventrally to the fin skeleton.
Before supplying the muscles, however, the ventral branches all run
into a longitudinal nerve, lying at right angles to their direction

(ventraler Längsstamm) from which the nerves to the muscles are given off. The dorsal branches behave similarly, but the arrangement is slightly more complex owing to the fact that two such longitudinal nerve stems are found, the "medialer" and the "lateraler Längs-stamm."* The ventral branch of the 40th nerve passes through the more medially situated of the two pelvic foramina before joining the longitudinal stem. The dorsal and ventral branches of nerves 31—39 are indistinguishable along the greater part of their course, as they all run together in a long nerve stem—the nervus collector— until just before the point where the girdle is reached. Here the dorsal branches contained in the collector separate from the ventral branches. The former are continued as a branch which runs into the dorsal "Längsstamm," whilst the latter pierces the more laterally situated of the two pelvic girdle foramina and enters the ventral "Längsstamm." The specimen described by Braus differs considerably, since (1) the nerves entering the fin are 25—45, (2) the girdle is pierced only by the 36th nerve which apparently corresponds to Davidoff's 40th nerve, and (3) the ventral branches of the collector do not pass through a foramen. These two cases alone are sufficient to show that a considerable amount of variation occurs.

The object of this investigation was to ascertain the range of such variations, and to endeavour to find out whether they afford any support or otherwise to either of the two theories which attempt to explain the varying position of the limbs in different species and in different members of the same species, *i.e.*, the theory involving verte-bral inter- or excalation and the theory of limb-migration. For this purpose a number of individuals of both sexes was examined, and the following points in each specimen accurately determined :—

(a) The serial number of the girdle-piercing nerves.

(b) The number of nerves forming the collector.

(c) The number of post-girdle nerves.

(d) The point of junction of the whole- and half-vertebræ ("Ganz- und Halb-Wirbel").

For the determination of the serial number of the nerves piercing the girdle the arrangement of the occipital region was in each case examined. This was found to be practically constant, thus affording a fixed point from whence to reckon. The nomenclature adopted for the nerves of this region is shown in fig. 1.†

The determination of the point of junction of half- and whole

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* *Cf. loc. cit.*, Taf. 29, fig. 15, and Taf. 31, fig. 27.

† This nomenclature has been adopted for convenience, and it does not neces-sarily follow that the nerve here denoted as *z* is homologous with the nerve similarly designated in other forms by Fürbringer and others. As Fürbringer's Memoir (8) is not accessible, I am unable to say at present whether for this species his *z* and my *z* are identical.

vertebræ presented somewhat more difficulty.   Over each centrum in
the trunk, and towards its caudal end, issue the dorsal and ventral
roots of a spinal nerve—the latter being rather more rostrally situated
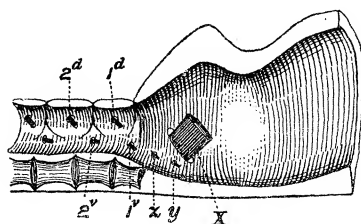than the former.   As the nerve whose ventral root issues between the

Fig. 1.—Hinder portion of skull and first few vertebræ.   Seen after a nearly
median sagittal section.

skull and first vertebra has been taken as z, it follows that the first
spinal nerve will issue out over the first centrum, the second nerve
over the second centrum, and so on.   This relation is always kept up
as we pass caudally along the vertebral column, *i.e.*, a nerve of any
given serial number always leaves the column over the caudal end of
a centrum having the same serial number.   When, however, we reach
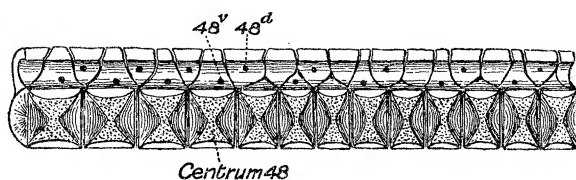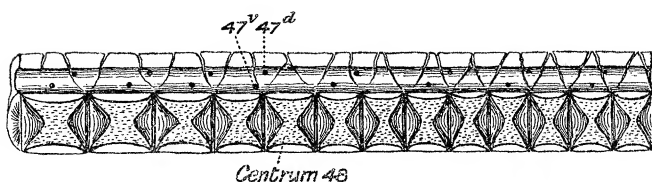a point on the vertebral column somewhere between the 45th and 50th

Fig. 2*a*.

Fig. 2*b*.

Two vertebral columns at region where the transition from half- to whole-
vertebræ occurs.   Seen from the inside after bisection and removal of the
dorsal cartilages of one side.

centrum we suddenly meet with a centrum over which there issues no spinal nerve (*cf.* fig. 2*a*, centrum 49). This centrum has been always reckoned as the first half-vertebra.

Of course it might be argued that in this particular instance centra 48 and 49 constitute the first two half vertebræ, and not centra 49 and 50 ; and similarly for all other cases.

Judging from analogous cases, such as that of *Amia calva* (Gadow 6, p. 202 and fig. 14), this latter view may possess rather more support. Until the question is settled by the investigation of the innervation of the myomeres in this region more cannot be said. The point of importance here is that a uniform system of nomenclature has been adopted for all the specimens examined. It may be mentioned that the mere size of the centra does not constitute an accurate indication of this point of junction. Though the first "halb-wirbel" centrum is usually smaller than that of the last " ganz-wirbel," yet a glance at fig. 2*b* will show that this is not always so. In this case centra 48 and 49 belong to the first half-vertebra in spite of the fact that centrum 49 is at least as large as any centrum of the whole vertebræ.

As the collector nerve lies along the outer side of the vena parietalis, injection of this with osmic acid rendered visible even the minutest branches which went to form it. The post-girdle nerves were also dissected with the help of the same reagent, which showed them up very readily in the fresh material used.

One hundred specimens in all were examined, of which fifty were males and fifty females. Of the males twenty-nine were adults ranging from 35 cm. to about 90 cm. in length, whilst forty of the females ranged between these sizes. The rest were old embryos about 25 cm. long, very nearly ready to be born, which for all intents and purposes, as will be seen below, could be reckoned as adults. The tabulated results of the points examined are given in Table I.

Table I.   Record of Points investigated in each specimen.

Nos. 1—50 are males; Nos. 51—100 females.   * denotes that the specimen is an older embryo.

No. of specimen.	Girdle-piercing nerves.	Post-girdle nerves.	No. of nerves to collector.	Whole vertebræ.
1	35	10	9	45
*2	35-36	10	11	46
3	35-36	10	11	46
4	35-36	10	11	46
*5	35-36	10	11	47
*6	35-36	10	10	46
7	35-36	10	9	45
8	35-36	10	9	45
9	35-36	10	9	46
*10	{ 35-36, 36-37 }	{ 11, 10 }	{ 12, 13 }	46
11	{ 36, 36-37 }	9	12	46
*12	36-37	11	12	48
*13	36-37	11	11	46
*14	36-37	11	9	48
15	36-37	10	11	48
16	36-37	10	11	47
17	36-37	10	11	47
18	36-37	10	11	47
*19	36-37	10	10	49
20	36-37	10	10	48
*21	36-37	10	10	47
*22	36-37	10	10	46
*23	36-37	9	12	47
*24	36-37	9	11	47
25	36-37	9	11	46
26	36-37	9	10	47
*27	36-37	8	11	46
*28	36-37	7	10	48
*29	37	9	10	47
30	37	9	10	47
31	37	9	10	47
32	37-38	10	11	46
*33	37-38	10	11	47
34	37-38	10	11	47
35	37-38	9	12	46
36	37-38	9	11	48
*37	37-38	9	10	47
38	37-38	9	10	47
*39	37-38	9	10	48
*40	37-38	9	10	48
41	37-38	8	12	46
*42	38	7	10	48
43	38-39	10	12	47
44	38-39	10	9	48
45	38-39	9	12	48
46	38-39	9	12	48
47	38-39	9	12	48
48	38-39	9	11	47
*49	38-39	9	11	51
50	38-39	8	{ 13, 12 }	47
51	35-36	9	9	46

Table I—*continued*.

No. of specimen.	Girdle-piercing nerves.	Post-girdle nerves.	No. of nerves to collector.	Whole vertebræ.
52	35–36	9	10	47
53	36–37	7	12	46
54	36–37	7	11	46
55	36	7	11	47
56	36	8	10	46
57	36–37	8	11	47
58	36–37	9	11	46
59	36–37	9	10	46
*60	36–37	9	11	47
61	36–37	9	9	47
62	36–37	10	9	45
63	36–37	10	10	46
64	{ 36–37 37	10 9	10 } 11 }	46
65	37	6	12	45
*66	37	7	11	46
67	37–38	8	11	46
68	37–38	8	10	46
69	37–38	8	11	47
70	37–38	8	11	47
71	37–38	8	11	47
72	37–38	8	10	47
73	37–38	8	12	48
*74	37–38	8	10	48
*75	37–38	8	11	49
76	{ 37 37–38	8 9	13 } 12 }	46
77	37–38	9	9	47
78	37–38	9	12	49
*79	37–38	10	11	48
80	38	7	11	46
81	38–39	7	11	47
82	38	7	10	47
*83	38	7	9	47
84	38	7	11	48
*85	38–39	7	9	48
86	38–39	8	9	46
87	38	8	10	47
88	38	8	10	47
89	38	8	12	48
*90	38–39	8	11	49
91	38–39	8	11	49
92	38–39	9	11	48
*93	38–39	9	11	50
94	38–39	10	11	49
95	{ 38–39 39	8 7	11 } 12 }	48
96	39	7	12	48
97	39	7	12	48
98	39	8	10	50
*99	{ 39–40 40–41	7 6	10 } 12 }	50
100	{ 39–40 } { 40 }	7	12	50

The range of variation with regard to the following points will be first examined, after which it is proposed to find out whether any correlations between the different parts can be established.

I. The serial number of the first girdle-piercing nerve.

II. The number of the post-girdle nerves.

III. The number of nerves forming the collector.

IV. Asymmetrical variations.

V. The number and position of the nerve canals.

VI. The number of the fin rays.

VII. The number of the whole-vertebræ.

I. *Variations in the Serial Number of the First Girdle-piercing Nerve.*

According to Davidoff's account the pelvic girdle is pierced by two foramina, through which pass the ventral elements of two consecutive fin nerves. Of these two foramina the more laterally situated is the larger, and affords a passage to the ventral elements of the nervus collector. Variations occur in this arrangement as will be seen below. In this paper the last nerve taking part in the formation of the nervus collector has always been regarded as the " first girdle-piercing nerve," though occasionally, as will appear below, the foramen through which it passes is no longer complete, but is reduced to a groove. The subjoined table shows the varying position of this nerve in the two sexes.

Table II.

Serial number of first girdle-piercing nerve.	♂.	♀.	
			Average for ♀ 37·25
			„ „ ♂ 36·43
35	19	4	
36	37	23	Diff. . . . . 0·82
37	26	31	(♂ being more rostral.)
38	18	31	
39	—	9	
40	—	2	

Since the serial number of the first girdle-piercing occasionally differs on the two sides of the same individual, each side has been given separately as an individual case. Consequently the 100 cases for each sex in the above table are taken from fifty specimens respectively. The chief point of interest here is that the males show a marked tendency to a more rostral position of the girdle, as compared with the females. This amounts to $37 \cdot 25 - 36 \cdot 43 = 0 \cdot 82$, or nearly a whole metamere.

II. *Variations in the Number of the Post-girdle Nerves.*

A considerable amount of variation occurred under this head, and the amount shown by the two sexes differs—the number in the male being greater than in the female. The results may be tabulated as follows :—

Table III.

Number of post-girdle nerves.	♂.	♀.	
			Average in ♂ 9·45
6	—	3	„ „ ♀ 8·06
7	4	28	
8	6	38	Diff. . . . . 1·39
9	38	24	
10	45	7	
11	7	—	

From this table it appears that there is a greater caudal extension of the fin innervation area in the male, which amounts to 1·39 metamere. It has, however, already been seen that in the male the pelvic girdle is on the average 0·82 metamere, more rostrally situated than in the female. Consequently the nett caudal preponderance of the fin innervation area in the male over that in female amounts to 1·39 − 0·82 = 0·57 metamere.

III. *Variations in the number of Nerves forming the Collector.*

Table IV.

Number of nerves forming collector.	♂.	♀.	
			Average for ♂ 10·70
			„ „ ♀ 10·69
9	12	14	
10	30	24	Diff. . . . . 0·01
11	36	42	
12	20	19	
13	2	1	

This table shows that, whilst the number of the nerves forming th collector is subject to a considerable amount of variation, there is a striking agreement in the average number of collector nerves in the two sexes.

IV. *Asymmetrical Variations.*

In five out of the hundred cases examined the pelvic girdle was
found to be asymmetrically placed (*vide* Table I, Nos. 10, 64, 95, 99,
100), that is to say, the serial number of the first girdle-piercing nerve
differed on the two sides.   I have already shown that the same
phenomenon occurs in *Mustelus lævis* ((12), pp. 335 and 343), and for
other groups it has been noticed more especially by Paterson ((3),
p. 522) in the case of man, and by Bumpus ((7), p. 465), and Waite
((9), p. 79) in the case of *Necturus.*   The last two writers suggest
that in *Necturus* such asymmetry may be due to the fact that the
curvature of the developing Amphibian embryo is lateral, seeking to
account in this way for the large number of asymmetrical variations
in the group, which amounts to 8 per cent.   Much stress, however,
cannot be laid on this, as Paterson has shown that asymmetrical
variations reach as much as $8 \cdot 3$ per cent in man, whilst among the
Elasmobranch the percentage reaches 5 per cent. both in *Mustelus* and
Acanthias.   Both these last groups differ from *Necturus* in that the
embryonic curvature is dorso-ventral instead of lateral.

V. *Variations in the Number and Position of the Nerve Canals.*

It has already been stated that there may be either, one or else two
nerve canals in the pelvic girdle.   These variations may be arranged
in three classes—fig. 3, A, B, and C.

Fig. 3.
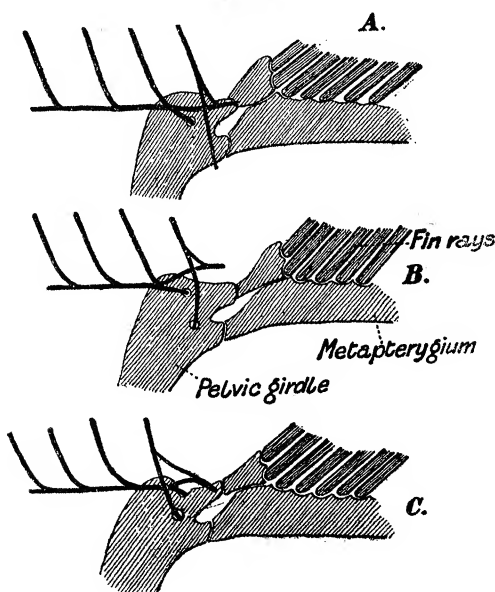
In A there is only one foramen, and through it pass the ventral branches of the nervus collector. In type B there are two foramina. Through the more lateral one pass the ventral branches of the collector, whilst the more median and posterior foramen gives passage to the nerve immediately succeeding the collector. This arrangement is the most usual one, and corresponds to that figured by Davidoff. In type C there is but one foramen, through which passes the ventral portion of the nerve succeeding the collector. The ventral division of the collector itself passes now through a more or less pronounced notch on the lateral border of the girdle.

Now according to the views of those who uphold the "side-fold" theory of limb origin, and explain the varying position of the girdle by assuming inter- or ex-calation of vertebræ, the pelvic girdle has been derived from the hypothetical segmental blocks of cartilage which were formed in the side-fold. As some of these coalesced and grew in medially to form the girdle they came to enclose the nerves which originally ran down between them. Consequently we may look to the nerves piercing the girdle as some guide to the number of morphological units which, on this theory, go to make up the girdle.

According to this view the girdle in *Acanthias* is composed of at least three such units (fig. 4, x, y, z). And to fit the facts it must be assumed that either x or z is capable of being dropped out. Consequently this theory involves the necessity of supposing that the pelvic
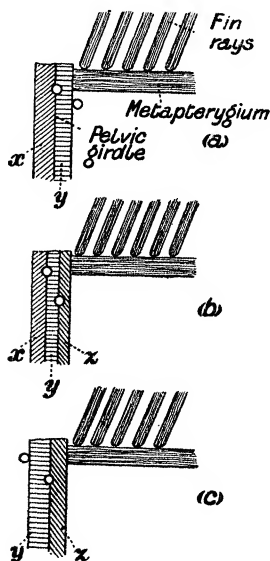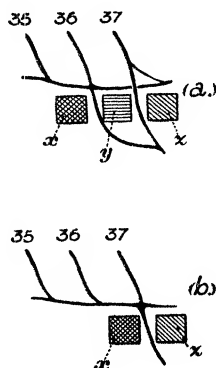

FIG. 4.

FIG. 5.

girdle is not homologous throughout the members of the same species, but that two-thirds of the morphological elements of the girdle are capable of undergoing some process of absorption. The capability of being absorbed possessed by the two outer elements of the girdle (x and z) will not, however, explain those instances where the girdle is asymmetrically situated. Take for example No. 64 (Table I). On one-side (fig. 5 (a)) the girdle is pierced by the 36th and 37th nerves. On the other side it is pierced only by the 37th (fig. 5 (b)). Now on the side-fold excalation theory the 37th and 36th nerves should bear the same relation to the three elements of the girdle. This can only be so if we assume that the middle element y has been dropped out. Consequently, in order to bring the theory into line with the different variations presented by the pelvic foramina and the nerves piercing them, we must assume that any of the three postulated elements of the girdle are capable of undergoing absorption, and, as has already been mentioned, we must further assume that a girdle which is pierced by one nerve is not homologous with a girdle pierced by two nerves. Also that a girdle pierced by one nerve is not necessarily homologous with any other that is also pierced by a single nerve (*cf.* fig. 4 (a) and (c)).

If, on the other hand, we seek to explain such variations on the migration theory we are not met with such difficulties. We may assume that the pelvic girdle in one specimen is strictly homologous with the girdle in any other specimen. We may suppose that the presence of one or of two nerve canals is determined by the position in which the "Anlage" of the girdle happens to be laid down. Thus in fig. 3, if we assume, for the sake of argument, that the most caudal nerve shown in each diagram is homologous, type C would result, if the "Anlage" of the girdle were laid down, in the most caudal of the three positions shown. If the "Anlage" be laid down a little more rostrally we should get type B; still more rostrally, and type A would result. Though it is possible that there may be some ontogenetic migration,* yet the facts are capable of explanation on this theory without the assumption of such a process. The matter has been discussed by Waite ((9), p. 86), who considers that in Necturus "the abnormal position of the girdle represents the development of a *new* girdle at a *new* point." The idea there discussed is similar to that given here with the exception of the *new* girdle. There seems to be no valid reason for supposing that the girdle in all cases is not a strictly homologous structure.

VI. *Variations in the Number of Fin Rays.*

The number of fin rays is subject to some variation. In order to ascertain whether there exists any correlation between the fin rays

* *Cf.* Braus (11), p. 588.

and the number of nerves innervating the fin—a correlation which on the side-fold excalation hypothesis we might be led to expect—I counted the fin rays in a dozen specimens of females. A small + after the number of fin rays denotes that it was uncertain whether an additional propterygial ray existed or not, the element in question being exceedingly small.

The result of the examination is given below :—

Table V.

Number of specimen in Table I.	Number of fin rays.	Number of nerves to fin.
59	16	19
55	16	18
63	16	20
61	16 +	18
52	17	19
71	17	19
89	17 +	20
51	18	18
56	18	18
80	18	18
81	18	18
95	19	19

A glance at the above table will show that there exists apparently no correlation between the number of fin rays and the number of nerves to the fin. Perhaps, however, it is best not to lay too much stress on this evidence, as the number of specimens examined is not very large.

VII. *Variations in the Number of whole Vertebræ.*

Mention has already been made of the way in which the point of junction between the half and the whole vertebræ was determined. The subjoined table gives the number of the whole vertebræ in the fifty specimens of each sex.

Table VI.

Number of whole vertebræ.	♂.	♀.		
45	3	2	Average for ♂	46·98
46	14	14	,, ♀	47·28
47	18	15		
48	13	10	Diff.	00·30
49	—	5		
50	1	4		

This table shows that on the average the male possesses 0·3 of a whole vertebræ less than the female.   It has already been shown that the position of the pelvic girdle in the male is on the average 0·82 metamere more rostral than in the female.   The interesting question of the correlation between the number of whole vertebræ and the position of the pelvic girdle, will be examined in more detail later on in this paper.

In bringing these statistics to a close, the question suggests itself— which of the two sexes is the more variable ?   To attempt to answer this, I have calculated the standard deviation (σ) and also the probability error (E) for the two sexes on the following points :—

Table VII.

	No. of cases in each sex.	♂.		♀.	
		σ.	E.	σ.	E.
Number of collector nerves	100	0·99	±0·066	0·96	±0·064
Number of post-girdle nerves.....	100	0·86	±0·058	0·96	±0·064
Number of whole vertebræ.......	50	0·98	±0·093	1·29	±0·122
Serial number of 1st girdle-piercing nerve................	100	0·99	±0·066	1·09	±0·073

From this table it will be seen that the variability of the female is greater on three of the above points, viz., with regard to (1) the serial number of the first girdle-piercing nerve, (2) the number of post-girdle nerves, and (3) the number of the whole vertebræ; whilst on the remaining point—the number of the collector nerves, the male shows a slightly greater variability, though here the two sexes are almost on an equality.   Of course it must be borne in mind that the numbers dealt with are small for applying this method.   Still the differences in the two sexes are fairly well marked, particularly in the case of the whole vertebræ, where the standard deviation in the female preponderates even when the maximum allowance is made in each sex for the probable error.

Having now concluded these statements on the amount of variation involved on the various points enumerated, we shall next enquire into the possibility of establishing any correlations between the position of the girdle and other points of variation.

A. *Between the First Girdle-piercing Nerve and the Number of Collector Nerves.*

As the nerves which take part in the formation of the collector are only concerned in the innervation of muscles connected with the most

rostral portion of the fin, it has not been thought necessary to consider the two sexes separately on this point. The following table shows the way in which the variations in the position of the first girdle-piercing nerve are associated with the variations in the number of the collector nerves.

Table VIII.

1st girdle-piercing nerve.	Collector nerves.					Total.	*Average.*
	9.	10.	11.	12.	13.		
35......	10	4	8	1	—	23	*10·00*
36......	6	19	26	8	1	60	*10·65*
37......	2	20	23	11	1	57	*10·80*
38......	8	8	21	11	1	49	*10·79*
39......	—	3	—	6	—	9	*11·33*
40......	—	—	—	2	—	2	*12·00*

From this table it will be at once seen that the more rostral position of the girdle is on the whole correlated with a reduction in the number of nerves taking part in the formation of the nervus collector. The only break in the ascending series of the average number of collector nerves as the girdle becomes more caudal, occurs where the girdle is pierced by the thirty-seventh and thirty-eighth nerves.

Here the average number of collector branches is practically identical in the two cases. The criticism may be made that a number of old embryos are included in the above table, and that, if we may judge from the case of *Mustelus* ((12), p. 335), these may show a larger number of collector branches than the adults, and so tend to bring irregularities into it. Such a criticism may be disposed of by the following two tables, in which a comparison is made between such embryos and the adults.

Table IX.

No. of collector nerves ..	9.	10.	11.	12.	13.	*Average.*
Embryos..............	6	23	26	6	1	*10·56*
Adults................	20	31	52	33	2	*10·75*

Table X.

First girdle-piercing nerve.	35.	36.	37.	38.	39.	40.	*Average.*
Embryos	7	23	18	32	1	1	*36·67*
Adults	16	37	39	37	8	1	*36·61*

These tables show that, whilst the serial number of the girdle-piercing nerve is identical, the average number of collector branches is slightly less in the embryos than in the adults.

Consequently, for practical purposes, such embryos may be considered as being of equal values with the adults. From analogy with the case of *Mustelus* quoted above, it might have been expected that these older embryos would have shown a slightly larger number of collector nerves than the adults. It must, however, be borne in mind that these embryos of *Acanthias* are rather more advanced than those of *Mustelus*, which were previously considered. As far as I have been able to observe, an *Acanthias* embryo of a given length about this stage is more advanced than a *Mustelus* embryo of the same length.

Returning now to Table VIII., if we are to explain the correlation there expressed on the side-fold excalation theory, we must suppose that the lesser number of collector branches associated with a more rostral position of the girdle is due to excalation of vertebræ through which pass nerves to the collector as well as vertebræ in the pre-collector area. This will be made clearer by the consideration of a concrete case. In fig. 6 two cases have been selected, one in which
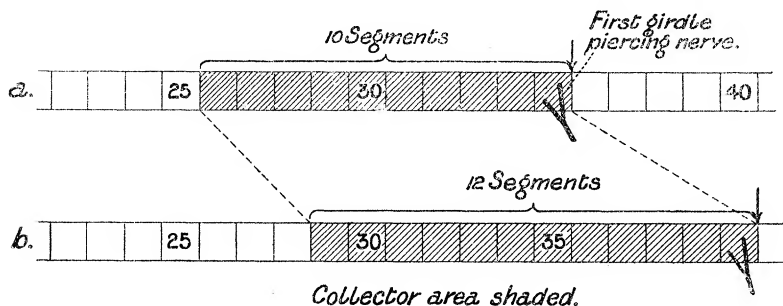

Fɪɢ. 6.

the first girdle-piercing nerve is thirty-five, and the other in which it is forty. From Table VIII. we learn that the average number of collector nerves associated with these two positions of the girdle are ten and twelve respectively. Now if we are to derive the case in which the girdle is more rostrally situated from that in which its position is more caudal, the figure shows that we must assume two segments to have been excalated in the collector area, and three in the pre-collector portion of the trunk. The assumptions made are (1) that the girdle-piercing nerve is homologous in each case, and (2) that a more rostral position of the girdle is in itself no argument for a lessened collector area. Consequently we must assume that on the side-fold excalation theory, excalation takes place both in the collector and the pre-collector areas.

On the migration theory, we should expect to find the more rostral position of the girdle associated with a lessened number of collector nerves. The reduction of the collector nerves, however, does not keep pace with the more rostral position of the girdle. From fig. 6 we see that with a change of five segments in the position of the girdle, there is associated a change of only two segments in the collector area. To explain this, we must suppose that those segments which lie just rostral to the collector area in the case where the girdle is more caudally situated, are capable of taking part in the collector when the girdle is shifted more caudally. Evidence in favour of such a view will be given later, when it is shown that in young embryos, the number of nerves forming the collector is greater than in the case of the adults (*vide* p. 19).

B. *Correlation between the First Girdle-piercing Nerve and the Post-girdle Nerves.*

It has already been seen (Table III) that on the average, the number of post-girdle nerves is considerably greater in the male than in the female. Consequently it has been found necessary to consider the two sexes apart on this point. The way in which the number of post-girdle nerves varies with the position of the girdle is shown in the following two tables :—

Table XI.

1st girdle-piercing nerves.	Post-girdle nerves 6.	7.	8.	9.	10.	*Average.*
35	—	—	—	4	—	*9·00*
36	—	6	4	10	3	*8·43*
37	2	2	19	6	2	*8·13*
38	—	12	13	4	2	*7·87*
39	—	7	2	—	—	*7·33*
40	1	1	—	—	—	*6·5*

Table XII.

1st girdle-piercing nerves.	Post-girdle nerves 7.	8.	9.	10.	11.	*Average.*
35	—	—	—	18	1	*10·05*
36	2	2	10	17	6	*9·62*
37	—	2	18	6	—	*9·16*
38	2	2	10	4	—	*8·88*

The tables bring out clearly the fact that, in both sexes, as the girdle comes to occupy a more rostral position, the number of post-girdle nerves shows a steady and marked increase. This is exactly what, on the migration theory we should expect to find. On the side-fold excalation theory, however, we should expect the position of the girdle to have no effect on the number of the post-girdle nerves. True, contraction of the fin may be going on, but even then there is no reason why the fins which show the greatest amount of contraction should be so regularly associated with a more rostral position of the girdle. The only way in which these facts can be explained on the excalation theory, is by assuming that the pre-girdle excalation which results in a more rostral position of the girdle, is accompanied by a post-girdle intercalation which leads to a greater number of post-girdle nerves. The greater the amount of pre-girdle excalation—the greater must we suppose is the amount of post-girdle intercalation.

C. *Correlation between the First Girdle-piercing Nerve and the number of whole Vertebræ.*

That there is a close correlation between the position of the girdle and the point where the whole vertebræ end is brought out by the following table:—

Table XIII.

1st girdle-piercing nerve.	Girdle whole 45.	46.	47.	48.	49.	50.	51.	*Average.*	Average number of post-girdle whole vertebræ.
35	6	13	4	—	—	—	—	*45·91*	10·91
36	2	24	22	10	2	—	—	*46·76*	10·76
37	2	15	24	12	4	—	—	*47·02*	10·02
38	—	4	16	19	6	2	2	*47·83*	9·83
39	—	—	—	5	—	4	—	*48·88*	9·88
40	—	—	—	—	—	2	—	*50·00*	10·00

From this table it will be seen that there is usually an interval of ten segments between the vertebra through which passes the first girdle-piercing nerve, and the last whole vertebra. This is especially well marked in the four most caudal positions of the pelvic girdle, *i.e.*, when the serial number of the girdle-piercing nerve is 37, 38, 39, or 40, the average number of whole vertebræ is exactly or very nearly 47, 48, 49, and 50 respectively.

Having just seen the necessity of assuming post-girdle intercalation to explain the larger number of post-girdle nerves associated with a

more rostral position of the girdle on the side-fold theory, we might expect to find some trace of this in the number of post-girdle vertebræ —that is, we might reasonably look for a larger number of whole vertebræ behind the girdle-piercing nerve when the girdle is situated more rostrally than when it is more caudally placed. A glance at Table XIII will show that this is only to a very small extent the case. Whilst the girdle shows a difference in position amounting to five segments, there is a difference of less than one between the average number of post-girdle whole vertebræ associated with its extreme positions.

On the migration theory such difficulties are not encountered. The comparative constancy in the number of post-girdle whole-vertebræ for all positions of the girdle is to be explained by supposing that there exists some relation between the position of the girdle and the point where that more flexible portion of the body—the tail with its half-vertebræ commences. The position where the " Anlage " of the pelvic fin is laid down must be supposed to determine, probably for mechanical reasons (*cf.* Gadow (6), p. 195), the point where the half-vertebræ shall start. Moreover, supposing the migration to be secondarily in a rostral direction helps us to understand why the number of post-girdle whole-vertebræ tends to be rather greater for the most rostral positions of the girdle, than for the intermediate or most caudal positions. We must imagine that the conversion of whole into half-vertebræ tends on the whole to keep pace with the rostral migration of the girdle. As the migration of the girdle attains its maximum the formation of half-vertebræ tends, so to speak, to lag behind, and as a consequence we find that in the most rostral positions of the girdle a rather larger average number of post-girdle whole-vertebræ.

Some Embryological Data.

The material used consisted of *Acanthias* embryos which had been preserved in corrosive sublimate and acetic acid. Horizontal longitudinal sections were cut through the pelvic area. These were treated with gold chloride and formic acid as described in a previous paper ((12), p. 344). Such portions of the plexus where the intercommunications of the nerves was required, were re-constructed on millimetre paper. The results may be tabulated as follows :—

Length and sex of specimen.	No. of nerves forming collector.	No. of nerves piercing girdle.	No. of post-girdle nerves.	No. of nerves forming posterior collector.
A. 31 mm. (?)	14	2	12	3
B. 32 ,, (?)	13	2	11	3
C. 42 ., (?)	12	{ 1 on left } { 1 on right }	11	3
D. 50 ,, ♀	—	2 (1st girdle-piercing nerve on left by groove)	10 (last small)	3
E. 62 ,, ♂	—	2	11	3 ⎤ Most caudal
F. 66 ,, ♂	—	2	11	2 ⎥ branches ⎬ much
G. 68 ,, ♀	—	2	11 ⎰ last two ⎱ very	3 ⎥ reduced except
H. 72 , ♀	—	2	11 ⎰ small	3 ⎦ in F.

In the younger stages, A—C, it is not possible to determine the sex as the mixipterygium is not yet distinguishable.   The table brings out the following facts :—

(1.) The number of nerves forming the nervus collector is greater than in older embryos or adults. This has also been shown by Braus for *Spinax niger* (11), p. 620, and by myself for *Mustelus lævis* ((12), p. 347).

(2.) The number of post-girdle nerves is greater in younger embryos than in older embryos or adults (*cf.* Table III).

(3.) The last two or three post-girdle nerves form a posterior collector (*cf.* (12), p. 347, and (11), p. 566), a structure which is quite separate from the "Langsstämme" occurring in the adults. These latter structures also are found in embryos of 42 mm. and upwards. In the two younger embryos (A and B) they are not yet fully formed (*cf.* fig. 7). I have only observed a posterior collector in one case among older embryos and never in adults. In the older embryo in which it occurred there were eleven post-girdle nerves, and the two branches of the posterior collector were extremely fine.

(4.) There is a certain amount of variation in the number of the pelvic foramina. Asymmetry occurred in one case, C.

The fact that the fin innervation area has a greater extent both caudally and rostrally in the embryo than in the adult, offers no criterion between the rival theories. On the side fold excalation theory we

should expect to find a greater rostral extension in the embryo, and
the greater caudal extension is also explicable on the assumption that
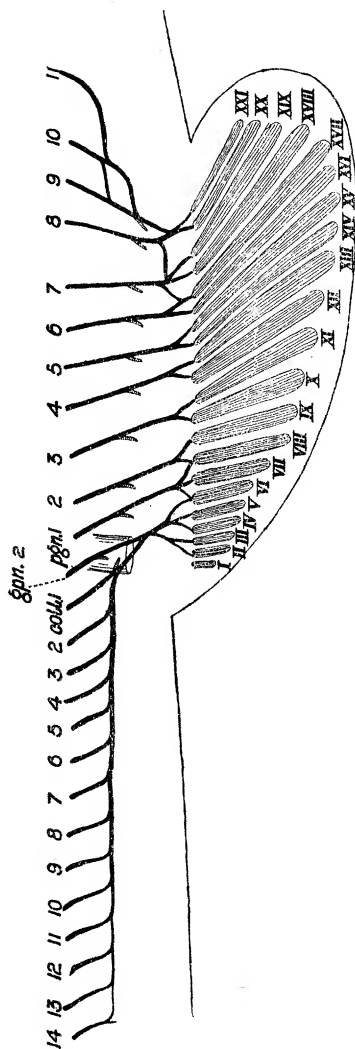a contraction of the fin area has also taken place caudally.

FIG. 7.—Diagrammatic representation of left pelvic fin and nerves in an embryo 31 mm. long. After reconstructions. The dorsal portion of the fin plexus is alone shown. The ventral branches are indicated in paler tint. The fin is supposed to be viewed from the exterior; the greater part of the girdle and the fin skeleton being removed. Fin muscles, parallel shading.

On the migration theory we have already (p. 17) found it necessary
to assume that one or two segments just rostral to the collector area in
the adult are potential collector segments. The greater number of
collector nerves in young embryos lends ample support to this view.

Again, since on this theory it is held that the formation of a collector

is due to migration of the fin, we must explain the presence of the posterior collector in the embryo as being due to a secondary rostral wandering of the fin.   In the case of *Mustelus* ((12), p. 348), it was shown that a portion at any rate of the nerves forming the posterior collector gave up this condition later, and ran down to the fin as separate nerves.   Now in the two male embryos, E and F, nerves 9, 10, and 11 of the post-girdle nerves form a posterior collector.   From Table III we learn that the average number of post-girdle nerves in the male is 9·45.   Consequently it is not unlikely that the more rostral of the nerves forming the posterior collector in the embryo will afterwards give up the collector condition and run separately to the fin.   Such a state of things would, as in *Mustelus*, be an argument for regarding the collector state as more primitive than the condition in which the nerves run down separately—which latter state is to be regarded as the more primitive on the side-fold theory.   Much stress, however, cannot be laid on this owing to the small number of the embryos examined.

Concerning the question of ontogenetic migration of the girdle no answer can be given in the case of *Acanthias vulgaris*.   When we take into account the great amount of variation which occurs in the adults, it is obvious that in order to obtain a satisfactory answer it would be necessary to determine the serial number of the nerves piercing the girdle in a large number of embryos, and to compare the mean with that of a large number of adults.   Such a course with the present methods of investigation would involve a labour of some years.   Consequently I have left it unattempted.   In the case of *Mustelus* a certain amount of evidence was collected which tended to show that no such process occurred ((12), p. 348).

Apart from the case of *Torpedo narce*, where both Braus and Mollier have agreed in considering that some such process occurs in the pectoral girdle ((11), p. 589 and following), the former has attempted to prove that ontogenetic shifting of the fin occurs in *Spinax niger*.

The evidence, however, is open to criticism since no account is taken of variation.   In support of such ontogenetic migration Braus adduces two pieces of evidence :   (*a*) during embryonic development a shifting occurs in the relation of the muscles to the nerves of the fin ; *e.g.*, a nerve which is an embryo of 2·6 cm. supplies muscles IX and X comes in an embryo of 3·2 cm. to supply muscles VIII and IX, and so on ((11), p. 568) ; (*b*) " die Nervenkanäle der Gliedmassengürtel schliessen während der verschiedenen Phasen der Entwicklung verschiedene seriale Nervenstämme ein " ((11), p. 588).   In a table on p. 620 Braus gives diagrams showing the condition of the plexus in adult and in four embryos of different stages after the formation of the fin skeleton.   He finds that in embryos of 31·5 and 32·0 mm., the girdle-piercing nerve is 29, in an embryo of 40 mm. it is 30, whilst in the adult again it

is 29. This he takes as evidence that the girdle migrates caudally between the stages of 32·0 and 40·0 mm. and then rostrally again between the stage of 40·0 mm. and the adult ((11), pp. 592, 593). To base such an important deduction on four specimens, whilst completely ignoring the possibility of his 400 mm. stage being merely a variation, seems greatly to weaken the case for ontogenetic migration of the pelvic fin in *Spinax niger*. Braus' argument rests on the assumption that no variations occur in the position of the girdle-piercing nerve in this species. Though I have never had an opportunity of examining *Spinax*, I have been able to make observations on a number of specimens of each of the following species—*Mustelus vulgaris, M. lævis, Acanthias vulgaris, Galeus canis, Carcharias glaucus, Scyllium canicula*, and *Scyllium catulus*. In all these species there occurred variations of several metameres in the position of the girdle. Until, therefore, it has been definitely shown that *Spinax* is constant with regard to the position of its pelvic girdle, any deductions based on the assumption that no variations occur in this species are to be accepted with the greatest caution.†

General Remarks.

As has already been stated, the idea with which this investigation was commenced lay in ascertaining the amount of variation shown on certain points in a given species from a given locality, and to discover how far these were explicable on either of the two rival theories—the side-fold theory and the migration theory of the origin of limbs.‡

It has been seen that certain of the facts are not in accord with the side-fold theory, without considerable strain on the imagination, though all are explicable on the theory of migration. Consequently the general tenour of the paper is on the side of limb migration.

* Twenty-three specimens obtained from Plymouth show a range of variation with regard to the girdle-piercing nerve, post-girdle nerves, and whole vertebræ amounting to four metameres. This species is the common form in the Channel. I have never been able to procure *M. lævis*, and according to Day ((2), vol. 3, p. 295) it does not occur here. At Naples, *M. lævis* is the common form, *M. vulgaris* being much scarcer. I have previously given evidence to show that *M. vulgaris* is a more stable form than *M. lævis* in the Mediterranean ((12), p. 342). We may look upon this as evidence for the greater variability of the more abundant form, or possibly we might regard the *M. vulgaris* of the Mediterranean as having acquired greater stability by the splitting off of a variable factor as *M. lævis*. This, of course, is mere speculation.

† Since the above was written I have had the opportunity of examining a number of specimens of *Spinax niger* on this point, and find that here, as in all other Elasmobranchs examined, there exist variations in the position of the pelvic girdle amounting to several metameres.

‡ This paper is not concerned with the more precise origin of the free limb, whether it has been derived from gill-arch rays, according to Gegenbaur, or from external gills, as recently suggested by Graham Kerr ('Proc. Cambridge Phil. Soc.,' 1899).

One fact, however, must be borne in mind. It has been assumed throughout that the vertebra and nerves of any given segment in one specimen are homologous with the vertebra and nerves of the segment with the same serial number in another specimen. In other words, to quote Bateson ((4), p. 32), " it has been assumed that the individuality of each member of the meristic series is respected." How far such a proceeding is justifiable is open to question. All that can be urged in support of it is, that firstly, we have been dealing with members of the same species all through, and secondly, that if the assumption is made, the variations under consideration no longer appear as a mass of disjointed facts, but group themselves with a certain coherence as the results of a process going on in this region of the body, a process of which we do not understand the cause, but to which has been given the term of limb-migration.

The facts recorded in this paper may be summarised as follows :—

(1.) Considerable variation occurs in *Acanthias vulgaris* with regard to—

> (*a*.) The serial number of the girdle-piercing nerves.
> (*b*.) The number of the post-girdle nerves.
> (*c*.) The number of nerves forming the collector.
> (*d*.) The number and position of the nerve canals.
> (*e*.) The number of the fin rays.
> (*f*.) The number of the whole vertebræ.

(2.) Asymmetry occurred in an appreciable number of cases.

(3.) Differences occurred in the two sexes on the following points. The position of the girdle was more rostral in the male than in the female. The post-girdle fin innervation area is greater in the male than in the female, owing to the development of the mixipterygium.

(4.) The female is on the whole more variable than the male.

(5.) A well-marked correlation exists between—

> (*a*.) The position of the girdle and the number of collector nerves.
> (*b*.) The position of the girdle and the number of post-girdle nerves.
> (*c*.) The position of the girdle and the number of whole vertebræ.

(6.) No correlation was found between the number of the fin rays and the number of fin nerves.

(7.) At certain stages in ontogeny the number of collector nerves is greater than in the adult.

(8.) At certain stages in ontogeny the number of post-girdle nerves is greater than in the adult. The most caudal two or three of these form a posterior collector—a structure which is never found in the adult

The facts recorded have been used as criteria between the two rival theories of limb origin with the following results :—

(1.) To explain the variations on the side-fold excalation theory, it must be assumed that excalation of segments is going on in the collector and pre-collector areas, whilst, at the same time, intercalation is taking place in the post-girdle area ; or, in other words, that the portion of the vertebral column in front of the girdle is tending to split up into fewer segments, whilst simultaneously that portion behind the girdle is tending to become divided into more segments. Leaving on one side the improbability of two contiguous portions of the vertebral column undergoing at the same time two opposite processes, an examination of the number of whole vertebræ associated with different positions of the girdle lends practically no support to the view that intercalation is going on in this area.

(2.) On the side-fold excalation theory an explanation of the variations in the position and number of the nerve canals of the girdle and of the occasional instances of asymmetry, necessitate the assumption that the pelvic girdle in different specimens is not homologous—an assumption which at present seems unjustifiable.

(3.) The different variations observed are not discordant with the view that the limb is capable of migrating along the body, on which view it must be supposed that a secondary rostral migration has followed a primary caudal one. Moreover, such a view receives confirmation from the existence of a posterior collector, and of a more extensive anterior collector in certain embryonic stages.

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" On the Application of Maxwell's Curves to Three-colour Work, with Especial Reference to the Nature of the Inks to be employed, and to the Determination of the Suitable Light-filters." By REGINALD S. CLAY, B.A., D.Sc. Communicated by Sir W. DE W. ABNEY, K.C.B., F.R.S. Received April 25, —Read June 20, 1901.

PART I.—THEORETICAL.

1. *Three-colour Projection.*

Maxwell showed that any colour in the spectrum could be matched by a suitable mixture of three monochromatic lights, red, green, and violet, and his celebrated curves give at each part of the spectrum the intensity of these lights necessary to imitate the colour at that point both in hue and luminosity. Other experimenters have since repeated his measurements with improved apparatus ; and throughout this essay I shall employ the curves found by Sir Wm. Abney as being probably the most accurate.†

Thus it is possible to photograph a spectrum in three colours only. Three negatives must be taken through "filters" which allow the colours to pass respectively in amounts determined by the above curves. One filter must allow light to pass according to the red curve, *i.e.*, the extreme red is just transmitted, and the bright red fully passed. Then the filter absorbs the yellow slightly, and the absorption increases along the spectrum, until in the blue and violet it is nearly complete. From this negative a transparency is made, and projected with red (monochromatic) light on a white screen. So for the green and violet. Assuming this done, we have a spectrum illuminated everywhere with the three monochromatic lights in the proportions indicated by the curves. Thus the spectrum will be reproduced exactly. (See Notes 1 and 2.)

If, instead of illuminating the three transparencies with mono-chromatic lights, we use red, green, and violet lights produced by passing white light through coloured glasses (providing that these lights are of the same dominant hue as the primary colour sensations), we shall still obtain a spectrum that appears almost correct. The light obtained by a coloured glass is not monochromatic, but, if the hue is

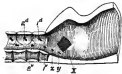† " The Colour Sensations in Terms of Luminosity," ' Phil. Trans.,' 1899.

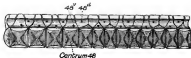Fig. 1.—Hinder portion of skull and first few vertebræ. Seen after a nearly median sagittal section.

Centrum 48
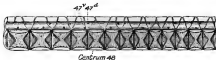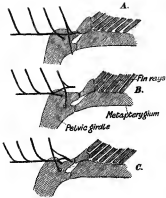
FIG. 25.

Centrum 48

FIG. 26.

Two vertebral columns at region where the transition from half- to whole-
vertebra occurs. Seen from the inside after bisection and removal of the
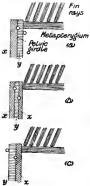dorsal cartilages of one side.

FIG. 3.

A.

Fin rays

B.

Metapterygium

Pelvic girdle

C.

Fin rays

Metapterygium

Pelvic
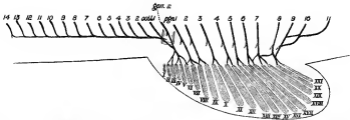girdle

x

y

z

(a)

(b)

(c)

FIG. 4.

FIG. 5.

FIG. 7.—Diagrammatic representation of left pelvic fin and nerves in an embryo 31 mm. long. After reconstructions. The dorsal portion of the fin plexus is alone shown. The ventral branches are indicated in paler tint. The fin is supposed to be viewed from the exterior, the greater part of the girdle and the fin skeleton being removed. Fin muscles, parallel shading.